

TROPHIC DYNAMICS IN AN ARCTIC LAGOON

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I. INTRODUCTION

Summer in the arctic is a brief but biologically active period. Large numbers of birds and fish migrate to the Beaufort Sea coast to feed on an abundant supply of aquatic invertebrates in nearshore waters. The present study examines major trophic pathways in one arctic coastal ecosystem--Simpson Lagoon in the Beaufort Sea, west of Prudhoe Bay. The approach used is to examine biotic components of the food web 'from the top down', that is, from consumers to producers. Thus, initial field studies focused on principal consumers (diving ducks and fish), followed by an examination of their invertebrate prey species, and finally an investigation of the carbon sources which drive the nearshore food web. The interdisciplinary overview of trophic dynamics presented in this paper is based on more detailed studies of birds (Johnson and Richardson, 1981), fish (Craig and Haldorson, 1981), invertebrates (Griffiths and Dillinger, 1981), and primary productivity (Schell et al., 1982) conducted as part of the Beaufort Sea barrier island - lagoon ecological process studies sponsored by the Outer Continental Shelf Environmental Assessment Program. Readers wishing more information on a disciplinary level are referred to the above reports.

II. STUDY AREA

Simpson Lagoon, located between Prudhoe Bay and the Colville River delta on Alaska's North Slope (Fig. 1), is a large and partially enclosed body of water measuring approximately 35 km in length and 3-6 km in width. It is a shallow water basin with an average depth of only 2 m (maximum 3 m). The lagoon floor is uniformly flat and almost featureless. In most areas, a layer of detritus covers substrates of mud and sand.

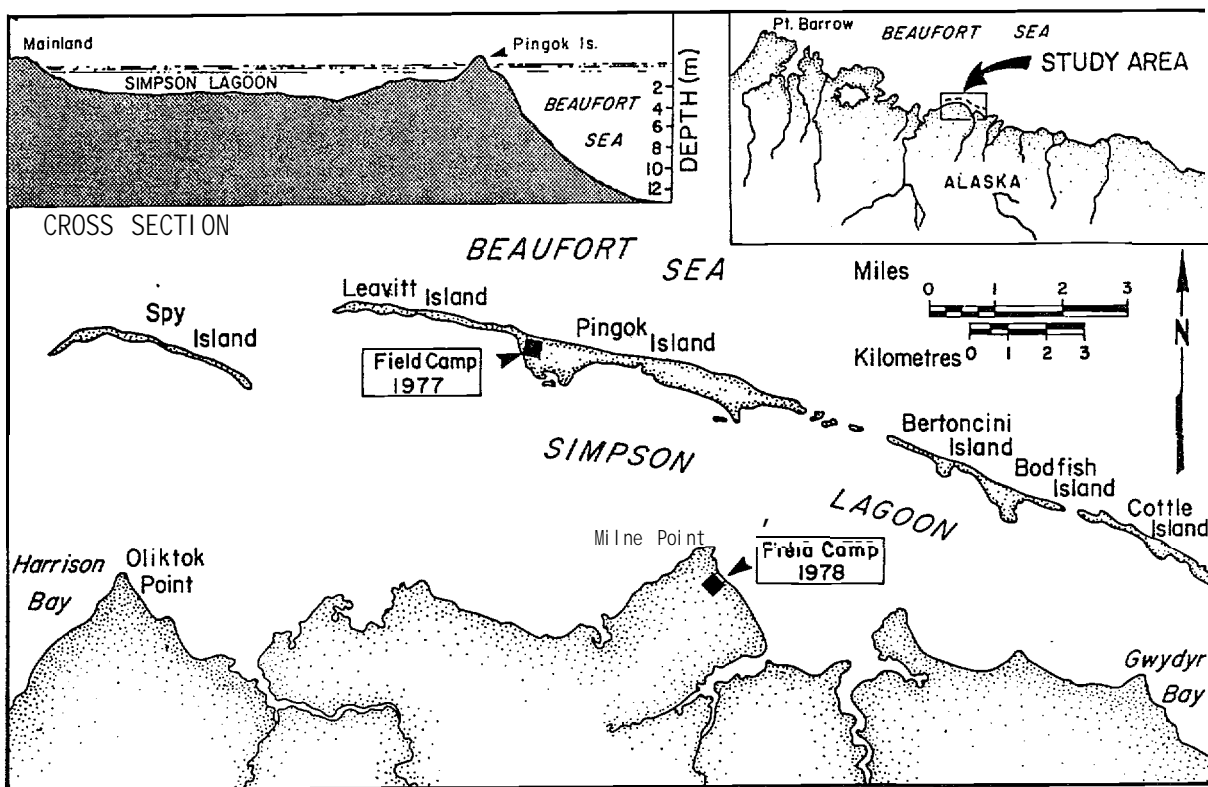


FIGURE 1. Simpson Lagoon study area on the Beaufort Sea coast of Alaska.

The ice-free period in the lagoon is short, lasting about 3 months (from early July to early October). The highly variable summer salinities (1-32 ppt) and temperatures (0-14°C) fluctuate as a direct influence of the prevailing westward flowing Beaufort Sea current, wind, and freshwater runoff. Lagoon waters are diluted by freshwater runoff and are correspondingly lower in salinity (usually 4-5 ppt) and higher in temperature (usually 2-4°C) than waters immediately seaward of the barrier islands. This difference is not as marked late in summer when runoff declines. Prevailing currents continually exchange lagoon water at an average rate of 10-20% d^{-1} and 100% d^{-1} when aided by exceptionally strong winds (65 km h^{-1} ; Mungall, 1978). During the winter, exchange diminishes substantially as surface ice steadily increases in thickness to about 2 m. By late winter (April) about 90% of the lagoon volume is frozen solid. Hypersaline conditions (up to 68 ppt; Crane, 1974) develop from salt exclusion during ice formation.

Additional details about the study area appear in Craig and Haldorson (1981).

A. *Biological Setting*

1. *Birds* . Over 100 species of birds have been recorded in the Alaskan Beaufort Sea area (Johnson *et al.*, 1975; Kessel and Gibson, 1978). However, many are briefly present as migrants, others are terrestrial species occupying tundra habitats, and a relatively small number of species of loons,

gulls, terns, and shorebirds and marine waterfowl occupy nearshore coastal lagoons during the summer.

In coastal waters, only the oldsquaw duck (*Clangula hyemalis*) and two species of phalaropes (the northern phalarope, *Lobipes lobatus* and the red phalarope, *Phalaropus fulicarius*) are found in large numbers for a substantial period of time (several weeks to months). Tens of thousands of oldsquaws are concentrated in coastal lagoons from mid-July to mid-August and again in late September as they molt and feed on marine invertebrates prior to their southward migration in fall. Similarly, juvenile phalaropes concentrate during August along lagoon beaches to feed on marine invertebrates prior to their fall migration. Hence, our investigations of avian consumers focused on these two key taxa which comprised the bulk of the avian biomass during the summer open water period in barrier island-lagoon systems. Glaucous gulls (*Lams hyperboreus*) were also sampled in 1977 but were subsequently not considered to be a key species due to their low numbers.

2. *Fish.* During the brief open-water season, the relatively warm and brackish waters of Simpson Lagoon and other nearshore waters provide important feeding habitat for anadromous and marine fishes. Over 30 species have been recorded in these waters but very few species account for the vast majority of fish present (OCSEAP, 1978). Key species are:

Species	Anadromous	Marine
Arctic cisco (<i>Coregonus autumnalis</i>)	x	
Least cisco (<i>C. sardinella</i>)	x	
Arctic char (<i>Salvelinus alpinus</i>)	x	
Fourhorn sculpin (<i>Myoxocephalus quadricornis</i>)		x
Arctic cod (<i>Boreogadus sa-ids</i>)		x

Seasonal use of nearshore waters by these fish differs.

The anadromous species arrive with the first signs of spring breakup, disperse along the coastline, and return to rivers or estuaries in fall to spawn and/or overwinter. Marine species tend to become more abundant in nearshore waters as the open water season progresses. While in nearshore waters, both anadromous and marine fish feed extensively on invertebrates, primarily mysids and amphipods.

Fish species composition and distribution change in winter. With minor exceptions, only marine species are present, and even these fish are eventually forced to vacate shallow areas as the ice thickens.

3. *Marine Mammals.* Marine mammals are not a significant component of the Simpson Lagoon fauna -- few were sighted during numerous aerial surveys of the lagoon.

4. *Invertebrates.* The invertebrate community in Simpson Lagoon is comprised of infauna (animals living within bottom substrate), epibenthos (animals usually living on or near bottom substrates), and pelagic forms (animals that inhabit

the water column). Due to lack of depth and rocky substrate, no kelp community is present in the lagoon. Abundant members of the infaunal group include bivalves (*Cyrtodaria kurriana*, *Yoldia arctica*) and polychaete worms (*Ampharete vega*, *Terebellides stroemi*). Infaunal organisms are restricted to the deeper (>2 m) portions of the lagoon because shallower areas (which account for approximately 35% of the lagoon area) freeze solid during winter. The epibenthos is dominated by amphipods (*Onisimus glacialis*, *Gammarus setosus*), mysids (*Mysis littoralis*, *Mysis relicta*), and the isopods (*Saduria entomon*). These animals are found throughout the lagoon during the open-water season and are generally associated with the detrital mat that covers large portions of the lagoon bottom. Pelagic forms common to Simpson Lagoon are copepods (*Calanus hyperboreus*, *Calanus glacialis*) and chaetognaths (*Sagitta elegans*).

The use of lagoon habitats by these three groups varies with season. Epibenthic and pelagic forms are generally excluded from the system in winter because much of the lagoon freezes solid. These forms recolonize the lagoon each spring and are abundant through the summer. Infaunal organisms and some amphipods are year-round residents in deeper areas of the lagoon which do not freeze in winter.

III. METHODS

A. *Vertebrate Studies*

1. *Birds.* Birds were collected by shotgun in Simpson Lagoon during the open-water seasons of 1977 and 1978 (Table 1). Oldsquaw ducks were collected in shallow water (average depth 2.1 m) during the periods 11 July to 14 September 1977 and 10 July to 27 September 1978. The general procedure for collection of specimens was to locate a flock and determine whether some birds appeared to be feeding (diving). Observers then sped into the flock and collected as many birds as possible. To mitigate postmortem digestion or regurgitation of any food items, the gut (proventriculus and ventriculus) and esophagus of each dead bird were injected with absolute isopropyl alcohol and the esophagus plugged with a paper wad. The proportion of oldsquaw containing identifiable food items in their stomachs was similar in both years (64-67%) and these adjusted sample sizes (i.e., excluding empty stomachs or those containing only unidentifiable material) are listed in Table 1.

Phalaropes and glaucous gulls were collected in shallow areas (<1 m deep) along shorelines and in bays where they feed. Phalaropes were collected 3 to 24 August 1977 and 6 August to 3 September 1978. Proportions of birds with identifiable food in their stomachs were 55% in 1977 and 44%

TABLE 1. Number of bird and fish stomachs (containing food) examined during summer and winter sampling periods.

	Summer 1977	Winter 1977/8	Summer 1978	Winter 1978/9	Summer 1979	Total
<u>Birds</u>						
Oldsquaw	54		72			126
Phalaropes	46		26			72
Glaucous gull	27					27
					TOTAL	225
<u>Fish</u>						
Arctic cisco	55	40	52			147
Least cisco	51	23	27			101
Arctic char	60		17			77
Arctic cod	34		20	84	47	185
Fourhorn sculpin	65	9		45		119
Boreal smelt				39		39
Arctic flounder			16			16
					TOTAL	684

in 1978. Because these two species were collected from mixed flocks feeding together, they were combined for dietary analyses. Glaucous gulls fed either singly or in loose aggregations, and they were not easily approached. Of the 28 glaucous gulls collected during 16 July to 19 September 1977, only one, which was collected at a mid-lagoon location, had an empty stomach.

2. *Fish.* The examination of fish feeding habits in Simpson Lagoon and surrounding waters was based on a sample of 684 stomachs of 7 species collected during summer and winter seasons 1977-79 (Table 1). All summer samples were from Simpson Lagoon in the vicinity of Milne Point and Pingok Island. Winter samples were combined from a wider nearshore region: arctic cisco, least cisco and fourhorn sculpin (Colville Delta, April/May 1978), fourhorn sculpin (Thetis Island, November 1978 and March/April 1979), boreal smelt (Simpson Lagoon and Thetis Island, November 1978) and arctic cod (Thetis Island to Narwhal Island, November 1978 and February 1979).

Fish used in diet studies were collected by gill net (87%) and fyke net (13%). Fish caught in fyke nets were used only when sample sizes from gill nets were low since those caught in fyke nets may have fed upon invertebrates attracted to or caught by the fyke net. For each species,

the fish examined were generally from the most common size-class present at the time of sampling (Craig and Haldorson, 1981). However, we exercised some selection of specimens to ensure that similar size-classes were studied throughout the summer months. Fish stomachs were preserved separately in formalin and later analyzed in the laboratory.

3. *Lab and Data Analyses.* Dietary analyses of bird and fish stomachs were based on wet weights of identifiable items, but the methodology differed between years. In 1977, weights were determined by directly weighing on a Mettler PL200 balance all identifiable specimens and fragments for each species or taxonomical group. In 1978 and 1979, weights of major prey species samples were determined by "reconstructing" their weight prior to partial digestion by the fish. This was accomplished by measuring a selected part of the organism and then calculating its total weight when ingested from length relationships between the part and the total organism, and from the weight-length relationship for the species. These methods, and their limitations, are more fully described by Griffiths and Dillinger (1981).

For detailed comparisons of fish and bird diets, prey items were analyzed in the following manner. Food items ingested by each predator were listed as percent wet weight of identifiable contents. Then, on the assumption that most

of the material not identified to the species level, e.g., "gammarid amphipods", was actually the remains of the identified gammarid species, the unidentified gammarids were allocated to the prey species known to be present in the proportions already determined for that predator. Laboratory taxonomists who identified these samples felt that the assumption was reasonable, although a small percentage of the broadly-based categories contained uncommon species. For the present uses of these data, it was felt that this procedure provides a better base for comparison than either deleting or retaining all broadly-based categories for mysids and amphipods. In any event, contributions of the broadly-based categories were generally small (usually less than 5% of contents).

Since a consumer's diet may change seasonally, a composite estimate of a species' diet was obtained by pooling and analyzing approximately equal numbers of samples collected during early, mid- and late periods of summer and winter, whenever possible. Since the variety of food items in stomach contents of individual fish was low (Fig. 2) and the relative proportions of major food groups did not vary greatly (Fig. 3), a sample of 10-20 stomachs appeared adequate to describe the kinds and proportions of important food items consumed by fish during any one sampling period. Actual sample sizes for fish were usually much larger than this (Table 1). For oldsquaw, it appeared that a sample

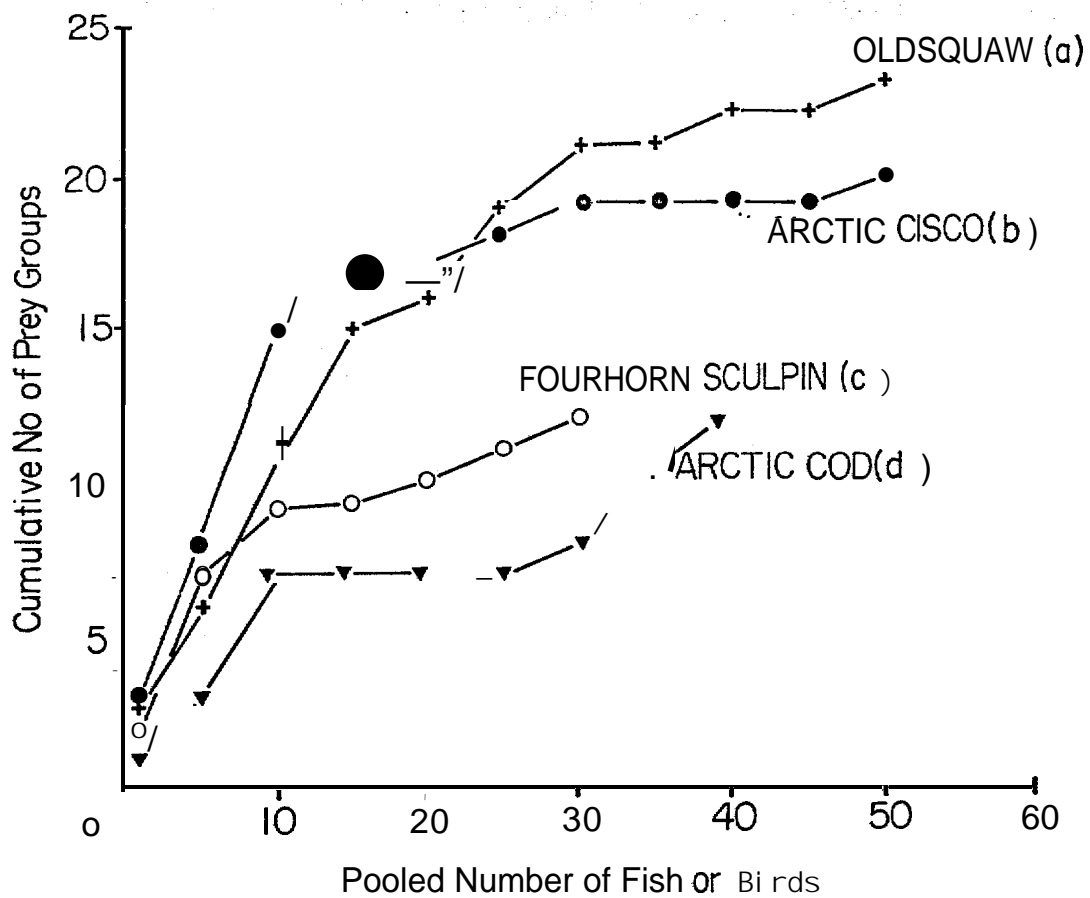


FIGURE 2. Cumulative number of prey in pooled oldsquaw and fish stomachs. Sample dates: (a, b) summer 1978, (c) April-May 1979, (d) February 1979.

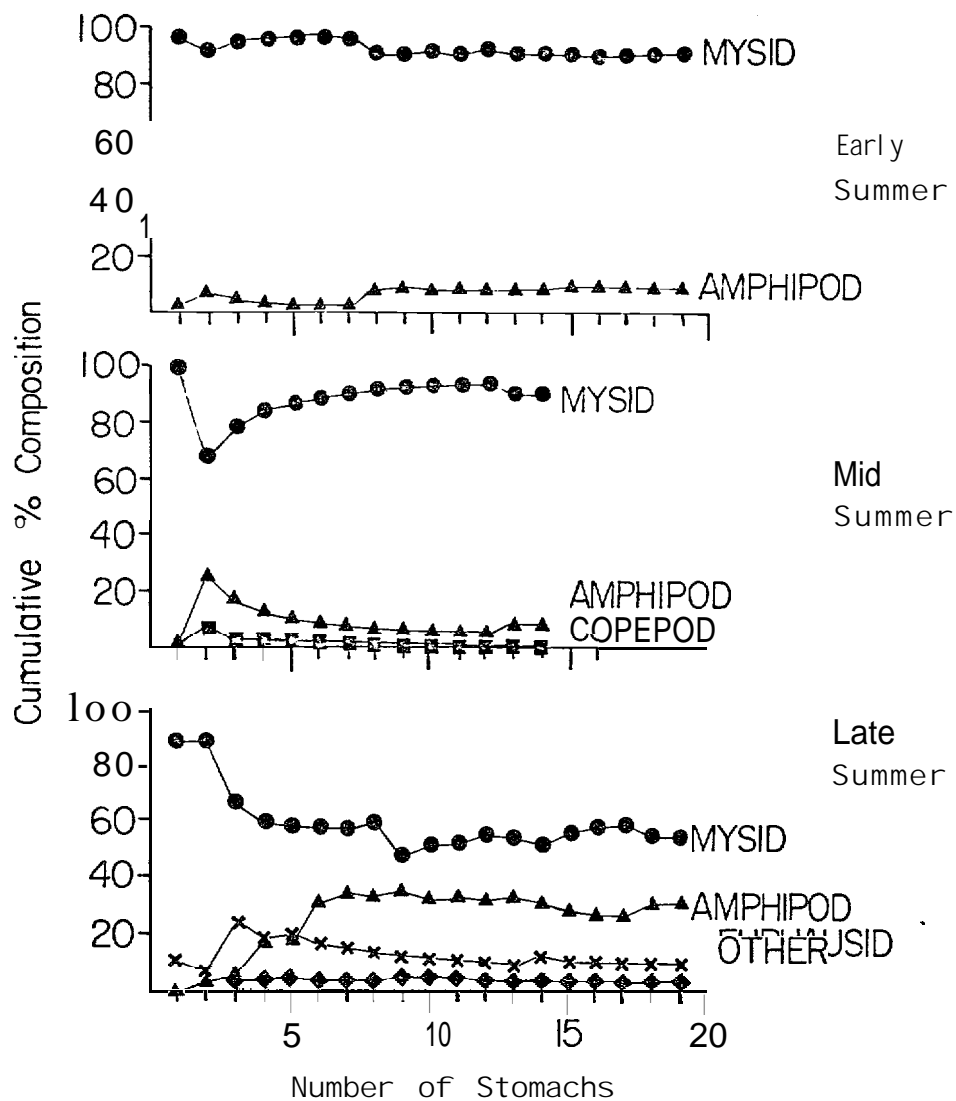


FIGURE 3. Cumulative percent composition (by wet weight) of major food groups in the diet of arctic cisco collected during three time periods during the 1978 open-water season.

size of ~~about~~ 30 birds (with food in their stomachs) was needed to adequately quantify the kinds of important food items consumed, and again, the actual sample sizes were larger. It is therefore felt that the pooled data from the summer or winter periods (depending on availability of specimens) reflected the general diets of each species in nearshore waters.

The degree of dietary overlap between bird and fish species was determined by the Schoener (1968) index:

$$R. = 1 - \frac{1}{2} \sum |P_{xi} - P_{yi}|$$

where P_{xi} and P_{yi} are the proportions of food category i in the diets of species x and y . Recent evaluations of several overlap indices indicate that Schoener's index is a generally preferred estimate of true overlap (Linton *et al.*, 1981; Wallace 1981). The index varies from 0, when the diets have no food items in common, to 1, when the diets are identical in kinds and proportions of food items. A value of 0.6 or greater is generally considered to be a biologically significant overlap (Zaret and Rand, 1971).

B. Invertebrate Studies

The invertebrate sampling program concentrated on organisms which were important foods for higher trophic levels (fish and birds) in Simpson Lagoon. Thus, sampling efforts

were directed towards **epibenthic** mysids, **amphipods** and copepods rather than **infaunal** organisms.

Sampling techniques differed in 1977 and 1978 because of findings in the first year of study and improvements implemented the second year. In 1977, three lagoon stations (Fig. 4) were sampled by a small otter trawl (4.9 m wide, 4 m long, 6.5 mm bar mesh cod end) and by SCUBA divers. Divers observed that the slow-moving trawl was not an effective method for capturing mobile **epibenthic** invertebrates. Diver transects, generally 25 m in length, were surveyed only in August. Along each of 12 transects, the diver made five estimates of the densities of mysids and **amphipods** in a 10 cm² area. The average of these estimates was extrapolated to 1 m² and converted to an estimated biomass of **epibenthic** invertebrates by using the 1978 ash-free dry weight for the predominant size classes of mysids and **amphipods** observed by the diver in 1977. For July 1977 and September 1977, the only available data concerning epibenthos were otter trawl samples. The following procedure was used to correct these results for underestimation of the biomass present. For each of mysids and amphipods, and separately for each of stations 1-3, the **July:August** and **September:August** ratios of wet weights in trawl samples were multiplied by the August estimate of grams ash-free dry weight m⁻² previously mentioned. A weighted mean for the whole lagoon was then determined for each sampling period (15 **July**,

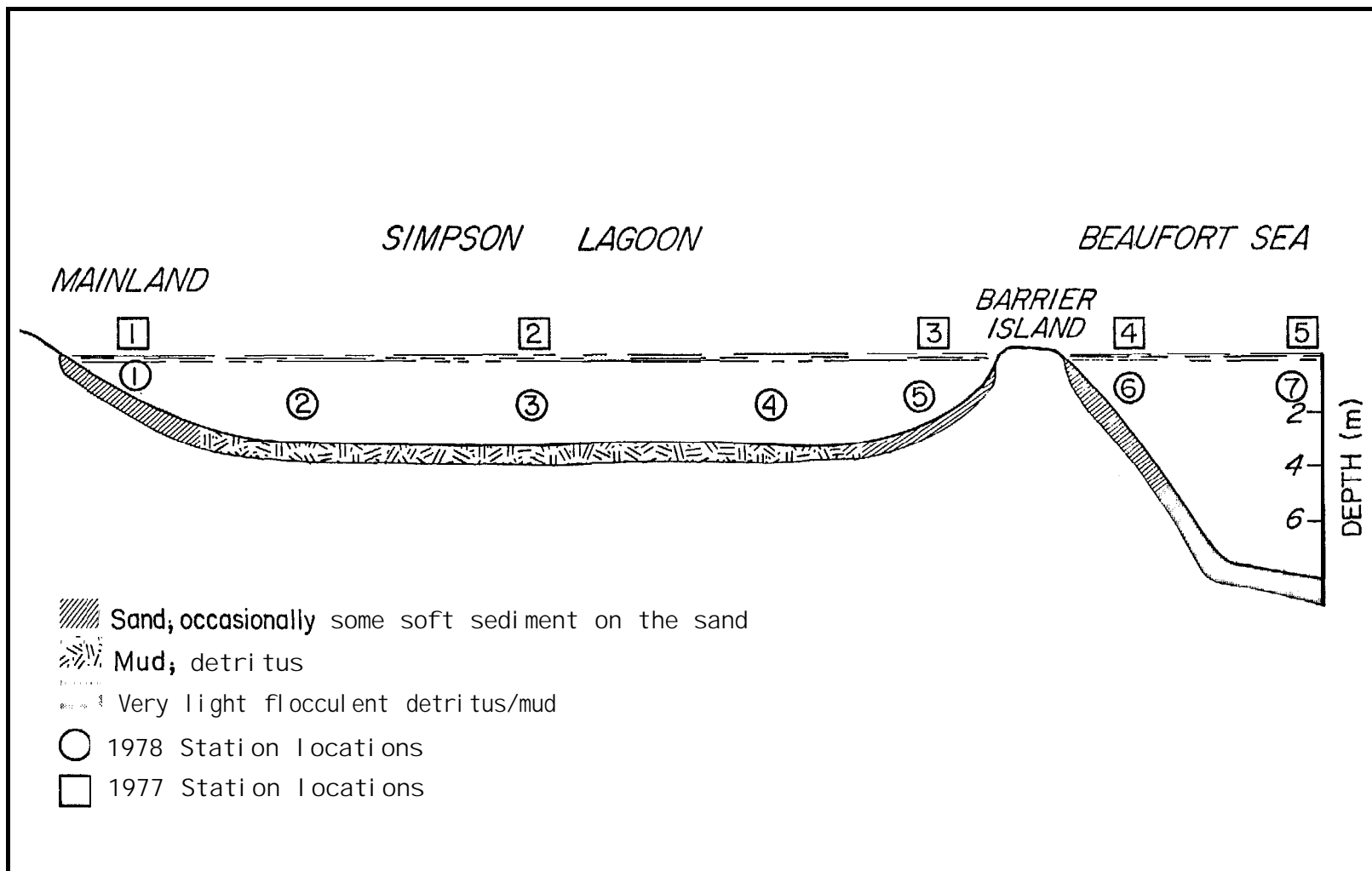


FIGURE 4. Schematic cross-section of Simpson Lagoon showing substrate types and invertebrate sampling stations for the open-water seasons of 1977 and 1978.

15 August and 15 September). The estimate for Station 3 on 15 September 1977 was not used as it appeared unrealistically high (68.7 g ash-free dry weight m^{-2}), possibly due to a sampling artifact (only one otter trawl sample was collected at this station and date). In this case, the weighted means for Stations 1 and 2 were assumed to apply to the entire lagoon.

In 1978, a central pursing drop net was designed for the project by modifying an epibenthic sampler developed by Clutter (1965). The net diameter was 0.5 m, height was 0.75 m, and mesh size was 1.0 mm. With both top and bottom ends of the net open, it was thrust by pole to the bottom in shallow water; in deep water the net was weighted to free-fall. Upon reaching the sea bottom, purse lines to top and bottom net openings were immediately pulled to enclose the sample in the net. Diver observations indicated that the net effectively captured epibenthic invertebrates. Five replicate samples were collected at each of seven stations in each sampling period, weather and ice conditions permitting (Fig. 4).

Organisms in the water column were sampled using a modified Faber net (0.5 m diameter, 1.024 mm mesh) (Faber, 1968). The net was towed for 5 minutes and the volume of water filtered was calculated using time and a flowmeter. Triplicate samples were obtained at Stations 2, 3, 4 and 7 in 1978.

c. *Carbon Sources*

1. *Phytoplankton Primary Production.* Productivity measurements were made using ^{14}C -uptake techniques (Strickland and Parson, 1972). Light intensities were adjusted to approximate in situ intensities and incubations were typically 4-6 hours. Although techniques varied somewhat between shipboard and shore incubations, the rates observed were consistent and agreed with literature values (Alexander *et al.*, 1975). The seasonal production estimates were more uncertain since very little data are available from June, early July and September. The techniques and caveats used in estimating seasonal production are discussed in Schell *et al.*, 1982, and Schell *et al.*, (this volume).

2. *Terrestrial Carbon Inputs and Consumer Production from Allochthonous Carbon.* Coastal erosion and fluvial transport deposit large quantities of terrestrially derived carbon in the lagoon environment, and quantitative estimates have been made by Cannon and Rawlinson (1978), and Schell *et al.*, (1982). Since the role of this energy source was uncertain, we compared the natural carbon isotope abundances of the organisms within the lagoon ecosystem with the carbon isotope abundances in the energy source materials (peat vs phytoplankton). The ^{14}C -depletions in the peat and $^{13}\text{C}/^{12}\text{C}$ ratios served as natural tracers of carbon from source materials to apical organisms

(Schell, 1982; Schell *et al.*, 1982) and enabled us to determine the critical energy sources supporting the fishes and birds.

IV. RESULTS

A. Vertebrate Consumers

i. *Trophic Spectrum.* In order to present an overview of food sources utilized by vertebrate consumers, we categorized the invertebrates and other potential food groups according to functional habitat or taxonomic units. This list included food groups known to be important to consumers in the study area and, for completeness, several basic food groups which are eaten by birds and fish in non-arctic areas. This range of foods potentially available to fish is called a trophic spectrum (Darnell, 1961) and the one used here is a slightly modified version used by Cailliet *et al.*, (1978).

Six general sources of food were recognized:

- (1) Water column organisms (including fish and zooplankton).
- (2) Mobile epibenthos (crustacea and polychaetes).
- (3) Sedentary epibenthos (crustacea, molluscs, tunicates and eggs from invertebrates or fish).
- (4) Infauna (worms such as polychaetes, and molluscs).
- (5) Flora (algae and vascular plants).
- (6) Other (detritus and miscellaneous).

When the **trophic** spectrum was examined, it was apparent that the diets of vertebrate consumers were surprisingly similar (Fig. 5). A single category, **mobile epibenthic crustacea**, was by far the most important food group for most fish and birds. This group accounted for over 90% of the diet for arctic **cisco**, least **cisco**, arctic char, arctic cod and **old-squaw**. The remaining predators fed heavily on this food category (44-64% of the diet) but additional preferences were also apparent. Two fed on "water column" organisms -- boreal smelt ate fish (41%), and **phalaropes** ate **zooplankters** (36%). Two predators fed on "sedentary **epibenthos**" -- **fourhorn sculpin** and arctic flounder ate a bottom crawling **isopod** (44%). **Glaucous** gulls had the most varied diet from the perspective of the **trophic** spectrum. These opportunistic feeders ate mobile and sedentary **epibenthos**, **small** fish and **birds**, and probably some camp garbage.

What was conspicuously **absent** among vertebrate consumers in the lagoon were species that rely on **infaunal** organisms, sedentary **benthos** or flora. This apparent void was **only** partly explainable by the reduced variety of organisms inhabiting rigorous environments **like** Simpson Lagoon. Harsh physical features of the **lagoon** (shallow and wind-churned waters, widely fluctuating temperatures and salinities, lack of solid substrates for attachment of plants or animals, and

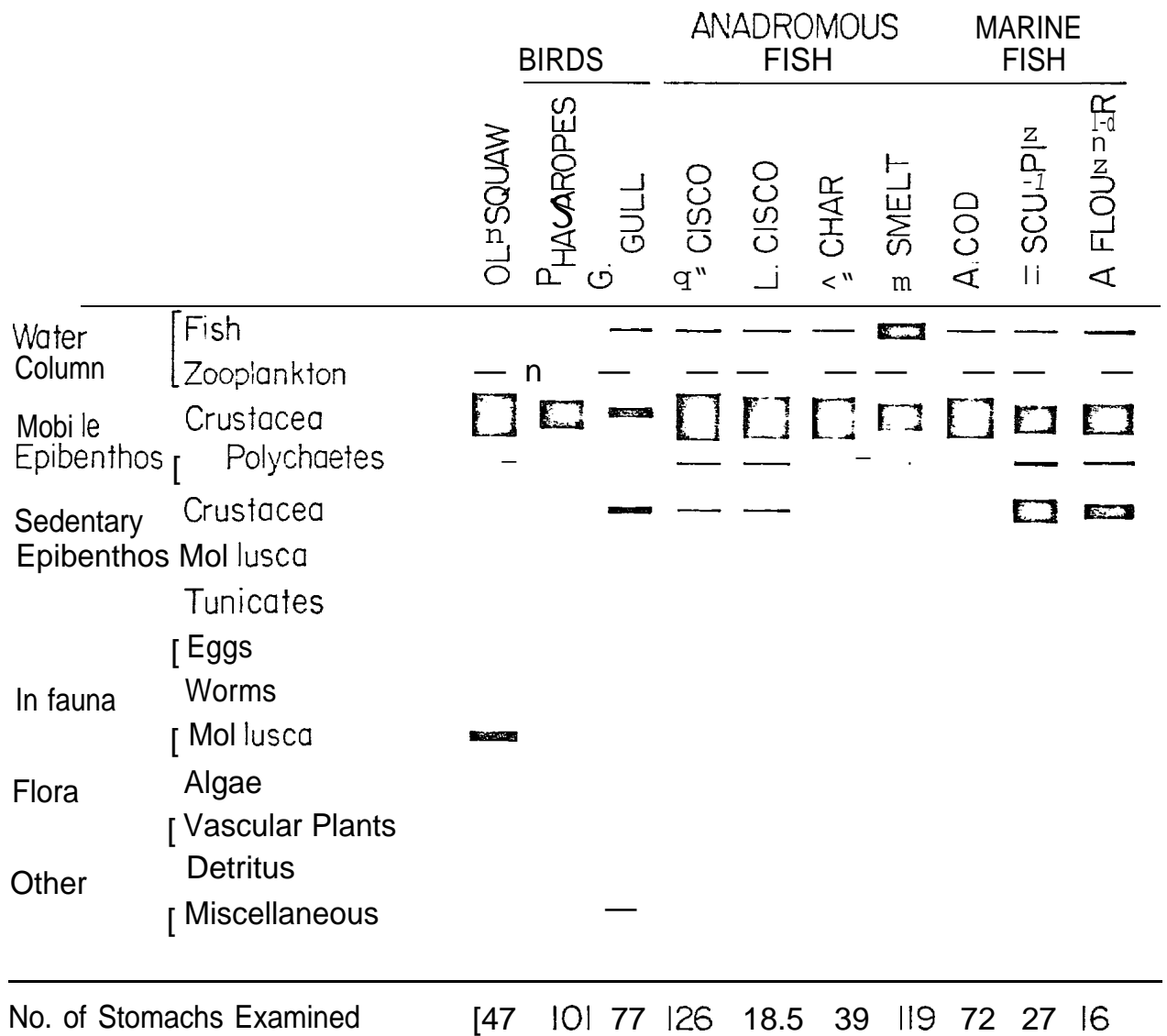


FIGURE 5. Trophic spectra of vertebrate consumers in Simpson Lagoon (combined dates and locations), 1977-9. For each species, proportions of foods in their diet are indicated by bands; the sum of heights of all bands within each spectrum equals 100%.

winter ice conditions) provided unsuitable conditions for all but a few kinds of organisms. There were, for example, no vascular plants growing in the lagoon, and very little macrophytic algae was present. However, a reduced variety of species does not, by itself, account for the observed reliance on mobile epibenthic crustaceans. Some infaunal organisms (bivalve molluscs, polychaetes) and sedentary epibenthos (isopods, tunicates, stalked polychaetes and hydroids) were relatively abundant but little utilized. Their biomass in Simpson Lagoon was similar to the biomass of the mobile epibenthic crustaceans:

	Biomass g m ⁻² ash-free dry weight
infauna and sedentary epibenthos	0.5a-2.1 ^b
mobile epibenthos	0.3-2.5 ^c

^a From Griffiths and Dillinger (1981) for bivalves excluding shells.

^b Recalculated from Crane (1974) for ash-free dry weight of worms, tunicates and bivalves excluding shells; deep lagoon stations, August 1971.

^c From Griffiths and Dillinger (1981); deep lagoon stations. August 1977 and August 1978.

It is understandable that some infaunal organisms were not vulnerable to predation by shorebirds due to water depth and lack of tidal exposure (daily fluctuations in water height are often only 10-15 cm), but this potential food source

appears accessible to diving ducks and fish. However, oldsquaw only ate them in early summer (approximately 10% of diet). Even the arctic flounder, a fish which may eat infaunal organisms (Andriyashev, 1954), fed primarily on amphipods and isopods in Simpson Lagoon. No bivalves were found in their stomachs, and polychaetes accounted for only 3% of their diet. A slight increase in use of infauna is conceivable if the polychaetes classified as "epibenthos" were actually "infauna" when eaten, but indirect evidence -- the lack of virtually any detrital material in fish or bird stomachs -- suggests this was not the case.

If alternate sources of food such as mobile epibenthic organisms are plentiful, there are reasons why a consumer might not seek infaunal organisms as part of its overall feeding strategy: (1) buried organisms may be hard to find, especially in shallow lagoon waters (less than 2 m deep) where the infauna is very sparse (Crane, 1974; Broad, 1978), or (2) prey size-classes vulnerable to predation may not be abundant or available at suitable depths.

2. *General Food Habits and Food Chain.* Mysids and amphipods were the most significant foods of birds and fish in Simpson Lagoon. During the 1977-1979 open-water seasons, these invertebrates accounted for over 90% of all identifiable food ingested by seven of the nine species examined at least during one of the years of study (Table 2). Copepods, isopods,

TABLE 2. Food groups eaten by lagoon birds and fish during the open-water period, 1977-1979.

% Composition (wet weight)																		
	Oldsquaw		Phalarope		G.	Gull	A. Cisco		L. Cisco		A. Char		Fourhorn Sculpin		A. Cod		Arctic Flounder	
Food Item	<u>77</u>	<u>78</u>	<u>77</u>	<u>78</u>	<u>77</u>	<u>77</u>	<u>78</u>	<u>77</u>	<u>78</u>	<u>77</u>	<u>78</u>	<u>77</u>	<u>77</u>	<u>78</u>	<u>79</u>	<u>77</u>		
mysid	68	80	8	2	7	70	87	69	66	16	89	10	88	38	59	1		
amphipod	16	12	20	96	23	25	11	21	33	78	4	81	9	18	39	58		
copepod	1	<i>a</i>	65	-	3	4	<i>a</i>	<i>9a</i>		1	<i>a</i>	<i>a</i>	24	41		<i>a</i>		
isopod	3	1	-	2	33	<i>a</i>	<i>a</i>	<i>a</i>	.	<i>a</i>	-	6	-	-	-	3	0	
fish	3	<i>a</i>	-	-	12	-	<i>a</i>	<i>a</i>	<i>a</i>	2	6	3	<i>a</i>	-	-	7		
bivalve	10	6	-	-	<i>a</i>	-	-	-	-	-	-		-	-	-	.		
other taxa ^b	<u>—</u>	<u><i>a</i></u>	<u>6</u>	<u>-</u>	<u>22</u>	<u><i>a</i></u>	<u><i>u</i></u>	<u><i>a</i></u>	<u><i>u</i></u>	<u>3</u>	<u><i>a</i></u>	<u><i>a</i></u>	<u><i>a</i></u>	<u>-</u>	<u><i>a</i></u>	<u>3</u>		
No. Stomachs Examined ^c	54	72	46	46	27	55	52	51	27	60	17	65	34	20	47	16		

^a <1.0%^b Includes: polychaetes, pteropods, cumaceans, chaetognaths, hydroi ds, decapods, euphausiids, birds
(eaten by glaucous gulls only)^c Stomachs containing food

bivalves and smaller fish were usually of secondary importance and the remaining groups (polychaetes, euphausiids, decapods, pteropods, cumaceans, chaetognaths and hydroids) were incidental food items. For oldsquaw and the two cisco species, proportions of the food groups eaten were generally similar between years of study. However, large changes in diet were noted for the phalaropes, char and cod. Phalaropes switched from copepods in 1977 to amphipods in 1978, and char switched from amphipods to mysids between years. Arctic cod ate varying proportions of mysids, copepods and amphipods.

In late fall and early winter, most of the vertebrate consumers emigrate from coastal waters of the Beaufort Sea. The birds fly to southern latitudes and most anadromous fish return to rivers to overwinter. Winter catches of fish in coastal waters consisted of only three abundant species: fourhorn sculpin, arctic cod and boreal smelt. In addition, arctic and least cisco and fourhorn sculpin were collected from the brackish waters of the Colville Delta. Stomach analyses showed that these fish continued feeding in winter and that mysids and amphipods were again heavily utilized (Table 3). Other foods were also important at this time. Fourhorn sculpin ate mostly isopods, and boreal smelt ate fish (arctic cod) .

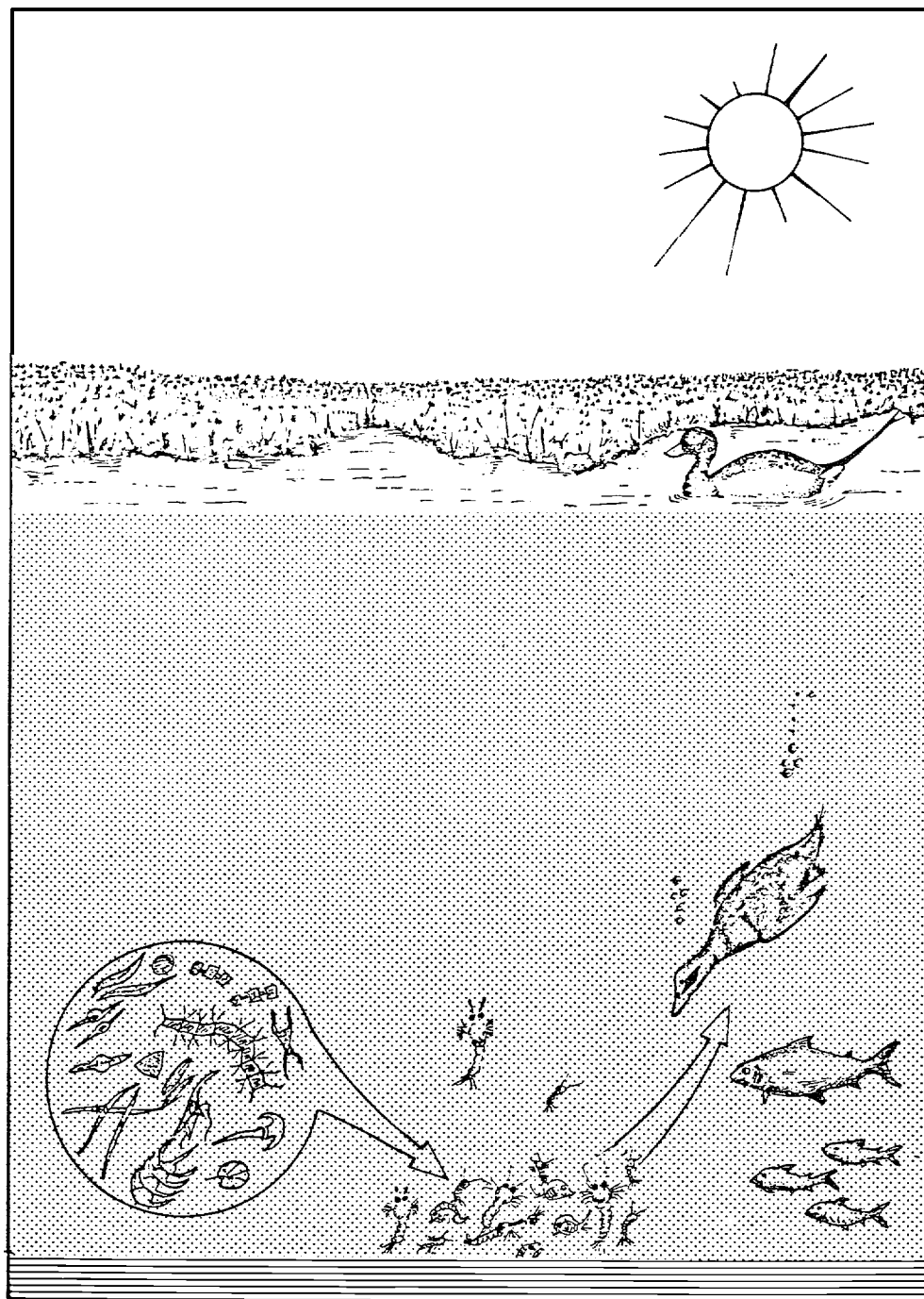
A generalized food chain for Simpson Lagoon is shown in Figure 6. The chain is very short. Fish and birds feed

TABLE 3. Winter foods of nearshore fishes, 1977-1979.

Food Item	% Composition (wet weight)					
	Colville Delta			Nearshore Waters		
	Arctic Cisco	Least Cisco	Fourhorn Sculpin	Fourhorn Sculpin	Arctic Cod	Boreal Smelt
mysid	a			3	93	39
amphipod	99	100	31	5	3	20
isopod			60	78	-	a
fish				a	2	40
fish eggs			9	5	-	-
polychaete	a			2		a
other taxa	a			6	2	a
No. stomachs examined ^b	40	23	9	45	84	39

^a <1.0%

^b Stomachs containing food.



PLANKTON

*EPIBENTHIC
//VERTEBRATES
(mysids, amphipods
and copepods)*

*VERTEBRATE
CONSUMERS
(fish and birds)*

FIGURE 6. Nearshore food chain.

primarily on epibenthic invertebrates (mysids and amphipods), and these invertebrates feed directly or indirectly on phytoplankton (discussed later).

3. *Principal Prey.* A list of prey for each consumer is presented in Table 4. Principal prey, arbitrarily defined as species or groups which constitute 10% or more (by wet weight) of the total diet, consisted of two mysid species, six amphipod species and four additional taxonomic groups -- copepods, isopods, bivalves and fish (Fig. 7). Several interesting points emerge in comparing diets among the consumers.

(1) The number of principal prey eaten by the common vertebrate species was low (2-7) during any single sampling period, reflecting considerable dietary overlap among predators.

(2) Two mysids, *Mysis litoralis* and *M. relicta*, were clearly the favored prey in the system. Of the 42 entries of principal prey shown in Figure 7 for summer and winter, the breakdown was:

	%
<i>Mysis litoralis</i>	29
<i>Mysis relicta</i>	21
<i>Onisimus glacialis</i>	17
<i>Pontoporeia affinis</i>	7
<i>Apherusa glacialis</i>	5
<i>Gammarus setosus</i>	5
Isopods	5
<i>Pontoporeia femorata</i>	2
<i>Gammarocanthus loricatus</i>	2
Copepods	2
Bivalves	2
Fish	2

TABLE 4. Modified list of foods in fish and bird stomachs whereby broadly-based categories (e. g., "unidentified gammarid amphipods") are converted to existing proportions of taxonomically-appropriate prey already listed (see text). Abbreviations: ARCS (arctic cisco), LSCS (least cisco, CHAR (arctic char), ARCD (arctic cod), FHSC (fourhorn sculpin), OLDS (oldsquaw), PHAL (phalaropes), BORS (boreal smelt).

Food Item	% Composition (Wet Weight)																	
	Summer 1977 ^b						Summer 1978						Summer 1979	Winter 1977-78		Winter 1978-79		
	ARCS	LSCS	CHAR	ARCD	FHSC	OLDS	ARCS	LSCS	CHAR	ARCD	OLDS	PHAL	ARCD	ARCS	LSCS	FHSC	FHSC	ARCD
<i>Mysis littoralis</i>	54.6	16.4	12.0	12.1	4.6	34.1	54.1	31.2	68.4	10.2	70.8	2.3	40.1	-	-	3.7	81.5	34.7
<i>Mysis relicta</i>	15.2	5.2	3.5	75.9	5.1	33.5	32.8	35.1	20.9	28.0	8.9	2.3	19.3	-	-	0.7	11.7	4.4
<i>Apherusa glacialis</i>	10.8	1.0	14.6	-	a	a	1.3	-	-	-	-	6.7	0.6	-	-	-	-	-
<i>Halirages mixtus</i>	-	-	-	-	-	-	1.6	-	a	-	-	-	a	-	-	-	0.4	0.3
<i>Onisimus glacialis</i>	12.4	8.0	11.5	7.0	47.8	8.0	6.7	24.8	2.7	17.5	10.4	82.4	35.4	-	-	0.8	1.5	0.5
<i>Gammarus setosus</i>	1.9	2.7	45.0	0.1	16.1	1.7	a	0.5	1.3	-	0.8	-	2.6	-	-	-	-	0.6
<i>Parathemisto</i> Spp.	0.1	a	5.0	1.8	4.2	4.9	1.7	-	a	-	0.3	-	-	-	-	-	-	-
<i>Pontoporeia affinis</i>	-	0.6	0.3	0.2	0.3	-	a	7.6	a	0.3	0.1	-	0.5	99.5	100	30.6	3.2	0.8
<i>Pontoporeia femorata</i>	-	1.9	0.2	-	0.3	-	-	-	-	-	a	-	a	a	-	-	4.2	0.4
<i>Gammarocanthus loricatus</i>	0.2	7.0	1.4	0.3	11.7	1.2	a	0.3	0.3	-	0.7	6.7	a	-	-	-	a	0.6
Copepod	4.5	8.7	1.3	2.1	a	1.2	0.6	-	-	44.0	a	-	0.9	-	-	-	a	0.2
Isopod	0.3	0.1	0.2	-	6.1	2.7	a	0.2	0.1	-	0.9	1.9	-	-	60.2	73.5	0.4	0.1
Cumacean	a	0.6	0.2	-	a	-	a	-	a	-	0.1	-	-	-	-	-	a	a
Euphausiid	a	-	2.8	0.5	-	-	0.7	-	-	-	0.1	-	0.4	-	-	-	-	-
Fish	-	0.3	1.6	-	3.3	2.7	0.2	0.2	5.8	-	0.4	-	-	-	-	-	0.7	1.5
Eggs	-	-	-	-	a	-	-	-	-	-	-	-	-	-	9.2	3.1	a	40.5
Bivalves	-	-	-	-	-	9.6	-	-	-	-	6.2	-	-	-	-	-	-	-
Polychaetes	-	-	a	-	-	-	-	-	0.2	-	-	-	-	-	-	-	-	-
Miscellaneous taxa	a	0.2	0.3	a	0.2	-	0.2	-	-	-	0.3	-	-	0.4	-	-	9.2	0.2
No. Stomachs	55	51	60	34	65	54	52	27	17	20	26	47	40	23	9	45	84	39

^a <0.1%

^b Detailed analyses of phalarope, glaucous gull and arctic flounder prey were not conducted in 1977.

PRINCIPAL PREY		SUMMER 1977						SUMMER 1978						WINTER 1977/8			WINTER 1978/9		
		A. CISCO	L. CISCO	A. CHAR	F. SCULPIN	A. COD	OLDSQUAW	A. CISCO	L. CISCO	A. CHAR	A. COD	OLDSQUAW	PHALAROP	A. CISCO	L. CISCO	F. SCULPIN	F. SCULPIN	A. COD	B. SMELT
MYSIDS	Mysis litoralis	•	•	•		•	•	•	•	•	•	•						•	•
	Mysis relicta	•	•			•	•	•	•	•	•							•	
AMPHIPODS	Apherusa glacialis	•		•															
	Onisimus glacialis	•		•	•				•		•	•	•						
	Gammarus setosus			•	•														
	Gammarocanthus loricatus				•														
	Pontoporeia affinis													•	•	•			
	Pontoporeia femorata																		•
							•												
BIVALVE																			
COPEPOD											•								
ISOPODS																•		•	
FISH																		•	

FIGURE 7. Principal prey ($\geq 10\%$ by weight) of nearshore birds and fish.

(3) The common vertebrate species tended to eat similar prey during the summer but different prey in winter.

B. Invertebrate Prey

From the foregoing, it is clear that mysids and amphipods play a major role in the nearshore foodweb. Observations by SCUBA divers provided an overall picture of the distribution and behavior of invertebrates in Simpson Lagoon. Divers found that mysids and amphipods were usually concentrated on or within 10-20 cm of the lagoon bottom. This observation was substantiated by quantitative sampling in the water column (plankton net) and on the lagoon bottom (drop net). Griffiths and Dillinger (1981) report that the average number of mysids and amphipods on the lagoon bottom far exceeded the total number of these organisms throughout the water column above. Though numbers varied by species and through time, the density of key invertebrate species was frequently 25 to 200 times greater in the region 0-20 cm above the lagoon bottom than in the entire 2 m of water above. The vertical distribution of prey is diagrammatically illustrated in Figure 8. It is thus apparent why these organisms are classified as "epibenthos" -- organisms generally living on or near bottom substrates. A detailed description of their temporal and spatial distribution in Simpson Lagoon is provided by Griffiths and Dillinger (1981).

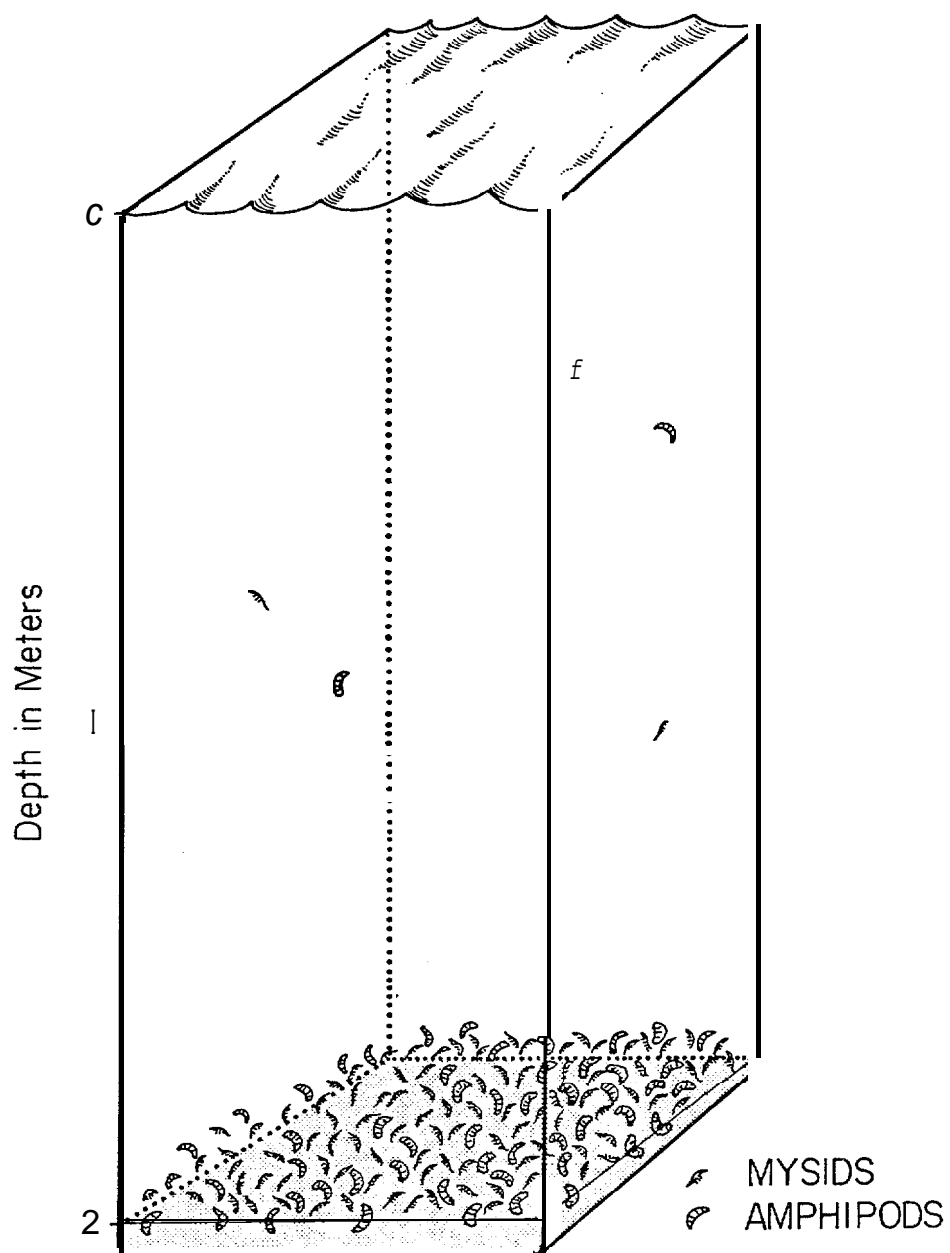


FIGURE 8. Schematic diagram showing the vertical distribution and relative abundance of invertebrates throughout the 2 m deep water column in Simpson Lagoon.

The food preferences of some of the epibenthic invertebrates themselves have been studied by Schneider and Koch (1979). Most species of epibenthic invertebrates in the study area appear to be trophic generalists:

Species	Principal Foods
Amphipods:	
<i>Onisimus glacialis</i>	Crustacean parts, Diatoms
<i>Onisimus litoralis</i>	Diatoms, Crustacean parts
<i>Gammarus setosus</i>	Peat, Diatoms, Crustacean parts
<i>Apherusa glacialis</i>	Diatoms, Dinoflagellates, Peat, Crustacean parts
Mysids:	
<i>Mysis relicta</i>	Peat, Diatoms, Crustacean parts
<i>Mysis litoralis</i>	Diatoms, Peat, Crustacean parts
Isopod:	
<i>Saduria entomon</i>	Diatoms, Polychaetes, Peat

The ultimate source of carbon for epibenthic invertebrates in the nearshore system is discussed later in this paper.

C. Trophic Relationships Between Consumers and Prey

This section compares the daily food requirements of fish and birds to the availability of their major foods (mysids and amphipods) during the open-water season. Since the fish and birds selectively utilize the lagoon in preference to the ocean, (Craig and Haldorson, 1981; Johnson and Richardson, 1981), only the feeding interactions within the lagoon were evaluated. However, as will be noted later, food appeared to

be equally abundant in the marine water habitats beyond the barrier island.

In the calculations that follow, it is apparent that we have obtained good estimates of some variables and less reliable estimates of others. While our results are affected by this variability in quality, the overall affect is thought to be small because density estimates of the dominant consumer (oldsquaw ducks) and prey (mysids and amphipods) are considered reasonably accurate. Estimates pertaining to fish are less precise but an error of even 100% in fish numbers or feeding rates would not greatly affect overall results as will be shown below.

Daily food requirements of the key vertebrates in the study area during both 1977 and 1978 were determined using bird and fish densities estimated by Craig and Haldorson (1981) and Johnson and Richardson (1981). Bird densities were determined by aerial surveys in both years (Table 5). Oldsquaw ducks were the prime avian consumers, and thus were the only bird species considered in this analysis. The 1977 and 1978 energy requirements for birds were computed using the following equation from Kendeigh *et al.*, (1977): at 0°C, $M = 4.142 W^{0.5444}$, where M = daily existence energy requirements during the molting period (Kcal) and W = weight of bird (g). A digestive efficiency of approximately 70% (Owen 1970)

TABLE 5. Estimated daily food requirements (mg ash-free dry wt. m^{-2}) of oldsquaw ducks in Simpson Lagoon in 1977 and 1978.

	1977		1978	
	no.	$km^{-2}{}^a$ $mg\,m^{-2}{}^b$	no.	km^{-2} $mg\,m^{-2}$
5 June	0.0	0.0	---	---
20 June	0.2	0.009	---	---
23 June	---	---	0.1	0.004
5 July	6.0	0.26	15.5	0.68
15 July	---	---	183.2	7.99
25 July	---	---	79.8	3.48
28-29 July	321.1	14.01	---	---
5 August	---	---	75.4	3.29
15 August	261.0	11.39	100.7	4.39
25 August	---	---	58.2	2.54
30 August	137.1	5.98	---	---
5 September	---	---	23.2	1.01
15 September	---	---	26.3	1.15
22 September	666.3	29.07	---	---
23 September	---	---	199.2	8.69

^aDensities are based on the results of aerial surveys and are weighted means for the lagoon (Johnson and Richardson, 1981).

^bFood requirements were calculated assuming 240 Kcal/bird-day as the gross energy needs of oldsquaw ducks (Johnson and Richardson, 1981). This was converted to mg ash-free dry weight by assuming that 5.5 Kcal is equivalent to 1.0 g ash-free dry weight.

was used in converting daily existence energy requirements to intake requirements.

Fish densities were determined primarily by sweeping a shoreline area of known size (1000 m^2) with a 91 m beach

seine. Density extrapolations to other areas in the lagoon were made using a correction factor based on the catch per unit effort obtained using gill nets in shoreline and offshore lagoon waters. Fish species (arctic and least cisco, arctic char, arctic cod and fourhorn sculpin) were combined to estimate densities of small fish (approximate average weight 15 g) and large fish (approximate average weight 470 g) in the lagoon in 1978 (Table 6). Fish densities for the previous summer were assumed to be similar with the exception that the run of millions of arctic cod encountered on 11-20 August 1978 did not occur in 1977 (Craig and Haldorson, 1981).

Energy requirements of fish were assumed to correspond to an intake of 6% of body weight per day for small fish, and 5% per day for large fish. The 6% figure was derived by Craig and Haldorson (1981) during a preliminary in situ experiment; the 5% figure is arbitrary but based on the general principle that energy requirements do not increase linearly with body weight.

For 1978, available biomass of mysids and amphipods was determined using results from the drop net samples. For each sampling date, the five lagoon stations were combined to produce a weighted mean for the entire lagoon (Table 7). Estimates for 1977 were less precise because a suitable epibenthic sampler was not available (see Methods).

TABLE 6. Estimates of daily food requirements (g ash-free dry wt^a m⁻²) of small and large fish in Simpson Lagoon in 1977^b and 1978.

Date	Lagoon Edge (6.9 km ²)				Lagoon Center (153.1 km ²)				Daily Ration (Weighted Mean) g m ⁻² x 10 ⁻⁴
	Small Fish (=15 g)		Large Fish (=470 g)		Small Fish (=15 g)		Large Fish (=470 g)		
	Density ^c	Ration ^d	Density	Ration	Density	Ration	Density	Ration	
	No. m ⁻² x 10 ⁻⁴	g m ⁻² x 10 ⁻⁴	No. m ⁻² x 10 ⁻⁴	g m ⁻² x 10 ⁻⁴	No. m ⁻² x 10 ⁻⁴	g m ⁻² x 10 ⁻⁴	No. m ⁻² x 10 ⁻⁴	g m ⁻² x 10 ⁻⁴	
Jul 01-10	5	0.5	5	14.1	0.5	0.1	0.5	1.4	2.1
11-20	20	2.2	20	56.4	2	0.2	1.5	4.2	6.7
21-31	50	5.4	40	112.8	5	0.5	4	11.3	16.4
Aug 01-10	50	5.4	40	112.3	5	0.5	4	11.3	16.4
11-20	1250 ^e	72.0	40	112.8	1200 ^e	69.1	4	11.3	84.9
21-31	70	7.6	40	112.8	7	0.8	4	11.3	16.8
Sep 01-10	100	10.8	40	112.8	10	1.1	4	11.3	17.2
11-20	100	10.8	10	28.2	10	1.1	1	2.8	5.4
21-30	100	10.8	5	14.1	10	1.1	0.5	1.4	3.5

^a Ash-free weight calculated by taking 12% (mean of mysids and amphipods) of wet weight.^b Density estimates for 1977 are assumed to be the same as 1978 less the arctic cod run 18-20 August.^c Density estimates from Craig and Haldorson (1981).^d Daily food rations (wet weight) are assumed to be 6% of body weight for small fish (Craig and Haldorson, 1981) and 5% of body weight for large fish.^e Food ration for this period is based on small fish approximately 8 g in weight (arctic cod).

TABLE 7. Estimates of food available (mysids and amphipods) in Simpson Lagoon in 1977 and 1978.

Station	Approximate Lagoon Area Represented, (km ²)	1977 (g AFDW m ⁻²) ^a						
		15, Jul	15 Aug	15 Sep				
1	36	0.12	0.33	0.24				
2	102	0.15	0.76	1.16				
3	22	<u>0.30</u>	<u>0.93</u>	<u>c</u>				
Total	160							
Weighted Means		0.16	0.69	0.92				

Station	Approximate Lagoon Area Represented (km ²)	1978 (g AFDW m ⁻²) ^a						
		8 Jul	19 Jul	03 Aug	18 Aug	30 Aug	14 Sep	23 Sep
1	36	0.11	0.16	0.22	0.068	0.06	0.27	0.25
2	34	0.12	0.23	0.37	0.30	0.20	0.33	0.18
3	34	0.04	0.39	0.19	0.66	0.18	0.20	0.23
4	34	^b	1.25	0.14	0.30	0.14	0.12	0.11
5	<u>22</u>	<u>0.029</u>	<u>0.12</u>	<u>0.10</u>	<u>0.09</u>	<u>0.04</u>	<u>0.06</u>	<u>0.01</u>
Total	160							
Weighted Means		0.079	0.45	0.22	0.30	0.12	0.21	0.17

^a Biomass is the sum of all mysids and amphipods in g ash-free dry weight m⁻².

^b Value at Station 4 assumed to be a mean of values at Stations 2 and 3.

^c Estimates for Station 3 on this date not used as they appeared unrealistically high (68.7 g m⁻²).

Comparisons of food available in the lagoon during 1977 and 1978 with the daily food requirements of the oldsquaw ducks and the major fish species using the lagoon are shown in Figure 9. The biomass available showed different trends in the two years. In 1977, there was an average of 0.6 g m^{-2} of food available which exceeded consumer requirements by about 50 times. In addition, the food supply increased in availability as the season progressed suggesting that food was not a limiting factor for fish and birds in the lagoon. In 1978, the food supply was again approximately 50 times greater than consumers required even though the available supply of food (0.2 g m^{-2} AFDW) was less than one half of that in 1977. Food requirements of oldsquaw in 1978 were generally lower than in the previous summer but fish densities and energy needs were greater because of a large influx of arctic cod in mid-August of 1978 (Table 6). Whether the year-to-year variations in numbers of consumers are related to differences in the energy available is not known.

In 1978 the energy requirements and food habits of *O. glacialis* were also considered since a large portion of the diet of this omnivorous amphipod consists of crustacean parts (Broad 1977; Broad *et al.*, 1979). Observations of feeding *O. glacialis* in aquaria and in the field indicated that they will readily consume mysids. Griffiths and Dillinger (1981) estimated the daily ration of mysids eaten by *O. glacialis* using

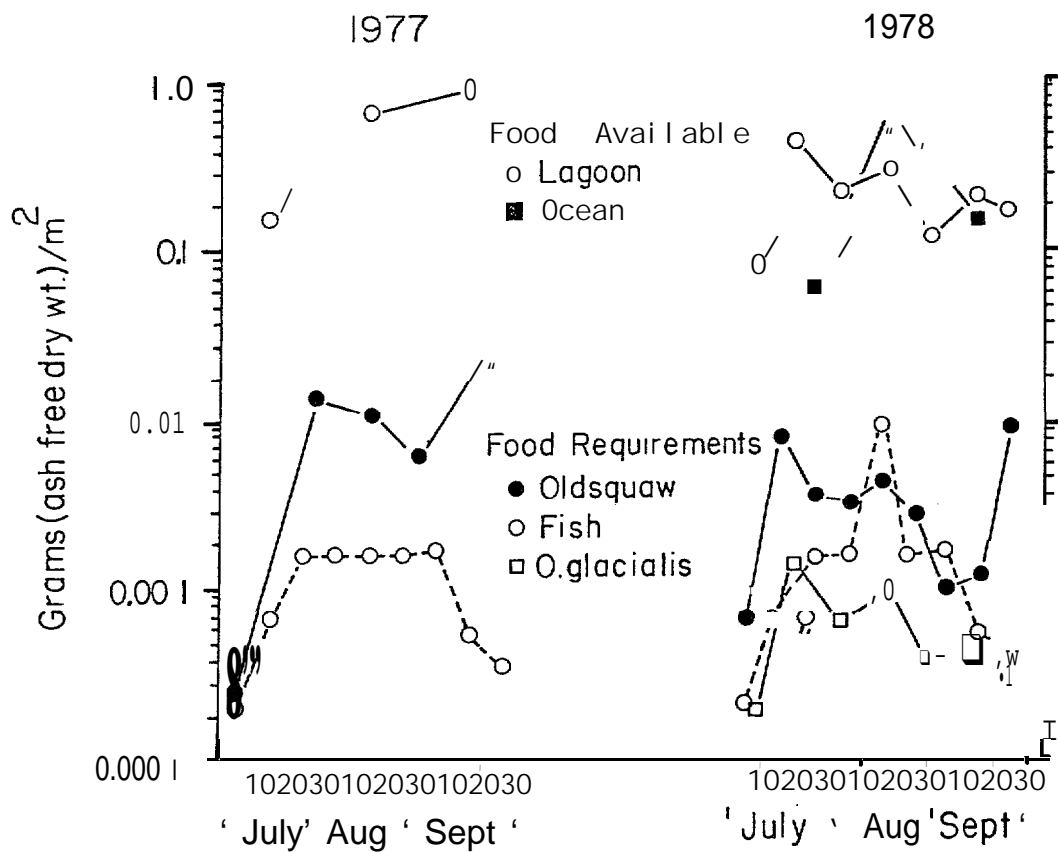


FIGURE 9. Comparison of food available (standing crop of mysids and amphipods) and the daily food requirements of birds (oldsquaw), fish (species combined), and predatory invertebrates (the amphipod, *Onisimus glacialis*).

the following findings and assumptions:

(1) An average daily increase in weight of 0.04 mg wet weight was determined for first year class individuals, the dominant size class in the lagoon.

(2) If we assume that this growth represents 10% of the food consumed (Parsons *et al.*, 1977), the daily food ration of *O. glacialis* is about 0.4 mg wet weight or approximately 0.08 mg ash-free dry weight.

(3) It was also arbitrarily assumed that only 10% of the diet of *O. glacialis* is comprised of mysids.

Using these estimates in conjunction with the weighted mean density of *O. glacialis* in the lagoon, we calculated the food requirements for this species in summer (Table 8). Even if only 10% of the diet of *O. glacialis* is composed of mysids, this predation represented a significant demand on the food resource, particularly when compared to the demands by the fish fauna (Fig. 9).

1. Maintenance of the Food Supply

The question arises as to whether the initial early summer movement of mysids into the lagoon, coupled with their growth during the summer, is sufficient to provide an adequate food supply for the consumers present (birds, fish and amphipods), or whether additional immigration is required throughout the open-water season to replenish the food supply. Since biomass

TABLE 8. Estimated daily food ration for *Onisimus glacialis* in Simpson Lagoon, 1978.

Station	Approximate Lagoon Area Represented (km ²)	Estimated Total Food Requirements (mg ash-free dry wt. m ⁻²)						
		<u>8 Jul</u>	<u>19 Jul</u>	<u>03 Aug</u>	<u>18 Aug</u>	<u>30 Aug</u>	<u>14 Sep</u>	<u>23 Sep</u>
1	36	0.5	1.3	0.8	0.1	0.5	0.1	1.2
2	34	1.1	0.2	1.3	1.4	0.8	1.0	0.6
3	34	0.2	1.7	1.7	2.7	1.9	1.3	0.8
4	34	^a	8.8	1.9	4.6	0.6	1.5	0.2
5	22	0.1	<u>1.8</u>	0.8	0.5	0.1	0.3	0.1
Weighted Means		1.9	13.9	6.5	9.3	3.9	4.2	2.9
Assuming Diet 10% Mysids Daily Ration of Mysids		0.19	1.39	0.65	0.93	0.39	0.42	0.29

^a Value at Station 4 assumed to be mean of values at Stations 2 and 3.

calculations do not permit a distinction between increases due to growth or immigration, we examined trends in the numbers of mysids present through the summer. During this period, no recruitment through reproduction occurs, and thus any variations in numbers of mysids in the lagoon must have been caused by a combination of immigration, emigration and/or cropping by predators. The numbers of mysids consumed by predators were calculated using the following assumptions:

(1) The mysid component of consumer diets was 80% for fish (Craig and Haldorson, 1981), 69% for birds (Johnson and Richardson, 1981), and 10% for *O. glacialis*.

(2) Fish and *O. glacialis* consumed sizes of mysids in approximately the same ratios that existed in the environment at any given time (Craig and Haldorson, 1981); oldsquaw ducks consistently selected mysids larger than about 10 mm (Johnson and Richardson, 1981).

(3) For consumers, the ash-free dry weight (AFDW) of mysids required during each interval between sampling periods was determined using the relationship:

$$\text{Required AFDW} = \frac{1}{2}(Y_1 + Y_2) (X) (\% \text{ of mysids in the diet})$$

where Y_1 = AFDW required at start of sampling period interval

Y_2 = AFDW required at the end of sampling period interval

X = number of days in the interval between sampling period

(4) For oldsquaw ducks, the required AFDW of mysids was converted to number of mysids by dividing by the AFDW of a 10.5 mm mysid. For fish and *O. glacialis* the numbers were obtained by dividing by the AFDW of an average mysid during each time period.

On the basis of these calculations, it is clear that the consumers would quickly deplete the available food supply if there was not a substantial and continual immigration of mysids into the lagoon (Fig. 10). The expected depletion rate of mysid populations for each time period suggests that even as late as 3 August, the density of mysids was not sufficient to maintain the predators until the end of the open-water season without new immigration.

It appears, then, that while Simpson Lagoon provides a good feeding area for large numbers of birds and fish, these consumers effectively crop the supply of mysids entering the lagoon. They would, in fact, deplete the lagoon of mysids if it were not for a continual replenishment of these prey organisms. The immigration of mysids, in turn, is likely a reflection of the high exchange rate of water in the lagoon with offshore or adjacent coastal waters. A hypothesis would thus follow that other arctic coastal habitats with limited water exchange may be less suitable as feeding areas for birds and fish.

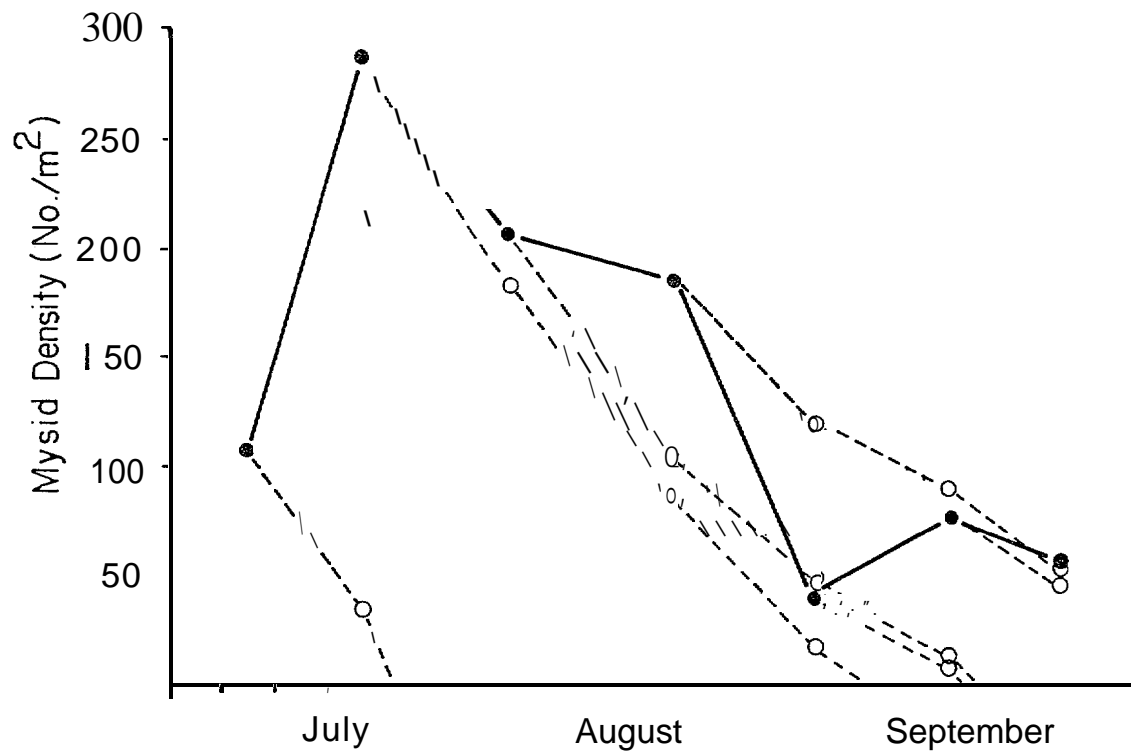


FIGURE 10. Observed density of mysids through summer 1978 (solid line) and expected rates of depletion at each date assuming only cropping by predators and no new immigration (dashed lines).

D. Carbon Sources

The energy **supply** required to support the **large** epifaunal populations **in** the **lagoon** could arise from three sources: in situ primary production, advection of primary production from offshore and inputs from terrestrial sources. A **small** component is **also** possibly derived from **longshore** transport of kelp (*Laminaria*) detritus from the Stefansson Sound area **east of** Simpson Lagoon although preliminary isotopic comparisons of invertebrate populations indicate that any inputs from this **source** are **small**.

Based upon natural carbon isotope abundances, we conclude that primary production, either in situ or advected, is responsible for approximately **90** percent of the carbon comprising the **amphipod** and **mysids** in Simpson Lagoon during the summer season. Peat carbon, as evidenced by radiocarbon depressions in consumers, is **less** than 10 percent in all invertebrate and fish samples from Simpson Lagoon. **Only** amphipods collected from near the mouth of the **Colville** River in late fall showed ^{14}C depressions equivalent to approximately 30 percent peat carbon (Schell *et al.*, 1982). The **large** quantities of peat in the river runoff and the very low primary productivity in the turbid river water account for the larger utilization in this area.

1. *Annual Primary Production Estimates.* Based upon literature estimates and our rate data which are listed in Table 9, we have extrapolated seasonal primary production by multiplying the average effective daylight hours for June through September and summing the monthly integrated amounts (see Schell et al., this volume). Within the Simpson Lagoon area, we estimate annual production to be 5-7 g C m⁻² or a total of 1.2-1.7 x 10⁶ kg C yr⁻¹. This contrasts with the approximately 24 x 10⁶ kg C yr⁻¹ derived from terrestrial inputs and dramatically illustrates the selectivity of invertebrate populations for phytoplankton carbon. Ice algae are not a major carbon source within the lagoon as the lack of light due to turbid ice and the shallow depths which result in large areas of bottom-fast ice all preclude the establishment of algal populations. We estimate a seasonal ice algal production averaged areawide of near 0.1 g C m⁻² yr⁻¹.

The data presented above can be used to compare the carbon requirements of consumer organisms with the sources available. Our calculations include mysids, copepods, amphipods and infauna as the major direct consumers of phytoplankton. Amphipods, especially *Onisimus* sp., are omnivorous and may be secondary rather than primary consumers of phytoplankton but for our calculations we used the assumption of Griffiths and Dillinger (1981) that 10 percent of their diet is animal material and the rest is plant derived. Table 10 lists the esti-

mated ingestion requirements based upon the assumptions below.

(1) Copepods

- (a) Average standing stocks in Simpson Lagoon during the summer are equivalent to 25 mg Cm⁻² (Griffiths and Dillinger, 1981).
- (b) Since limited data are available on winter standing stocks we assume the summer data are representative of the period July-November and that populations decrease to an average value of approximately five percent of summer (Tarbox *et al.*, 1979).
- (c) We convert standing stocks to ingestion rates by assuming that copepods ingest 40 percent of their body weight per day (Parsons *et al.*, 1977) and that the same percentage of body carbon is ingested.

(2) Mysids and Amphipods

- (a) Total population growth is calculated from the seasonal mysid and amphipod densities and the growth equations for first-year class *Mysis litoralis* and *Onisimus glacialis* since these are the dominant species present (Griffiths and Dillinger, 1981).
- (b) Growth is related to ingestion using a gross growth efficiency of 10 percent (Parsons *et al.*, 1977).

(3) Infauna

- (a) Infaunal biomass is about the same as epifauna (Crane and Cooney, 1975, and this paper) so we have assumed that infauna ingest the same amount of carbon each year as mysids and amphipods. Food is assumed to be sinking phytoplankton or fecal pellets derived from phytoplankton.
- (b) The summer ingestion rates are assumed to be twice the winter rates due to temperature and salinity changes.

From the results in Table 10, we calculated the total amount of carbon ingested each year by secondary consumers to be approximately 6.7 g Cm⁻². This was based upon food requirements for amphipods, copepods and infauna derived from

TABLE 9. Monthly averaged primary productivity estimates from ^{14}C incubations for Harrison Bay, Simpson Lagoon, Prudhoe Bay and Offshore.

Study Area	Investigator	Averaged Primary Productivity Values ($\text{mg C m}^{-3} \cdot \text{hr}^{-1}$) ^a			
		May	June	July	August
Harrison Bay	Alexander <i>et al.</i> (1975) This study				0.61 0.28
Simpson Lagoon	This study Alexander <i>et al.</i> (1975)		0.18	1.86	0.33 2.27
Prudhoe Bay	Coyle (1974)			3.46	0.77 0.48
Offshore	Homer and Schrader (1981) Schell <i>et al.</i> (1982) Alexander <i>et al.</i> (1975)	0.07	0.09 0.15	1.89	2.39

^aNo data available for September from nearshore waters. Average productivity rates from August ($1.0 \text{ mg C m}^{-3} \cdot \text{hr}$) were used. Offshore values are from stations less than 10 km north of the barrier islands of Simpson Lagoon and Stefansson Sound.

TABLE 10. Carbon ingestion by secondary consumers in Simpson Lagoon.

Group	Ingestion (g C m^{-2})			Total
	July- Sept	Oct- Mid-Feb	Mid-Feb- June	
Copepods	0.9	0.6	0.1	1.6
Mysids	1.1	0.2	0.1	1.4
Amphipods	0.5	0.6	0.2	1.3
Infauna	1.0	0.8	0.8	2.6
Totals	3.5	2.2	1.2	6.9

average annual densities in Simpson Lagoon. If these organisms have assimilation efficiencies near 60 percent (Parsons *et al.*, 1977), their carbon assimilation is $4.1 \text{ g C m}^{-2}\text{yr}^{-1}$. We estimate annual primary productivity in Simpson Lagoon to be $5\text{--}7 \text{ g C m}^{-2}\text{yr}^{-1}$ from the data of Alexander *et al.* (1975), and therefore, find ecological efficiencies of 60–80 percent. These values are higher than the usual 20 percent (Parsons *et al.*, 1977) but are certainly within the range one might expect considering the assumptions and data available. It would seem then that the primary and secondary productivity data appear to balance.

2* *Transport of Primary production into Lagoon.* The finding that terrestrial carbon does not support the epibenthic fauna of Simpson Lagoon to an appreciable extent underscores the close links between the summer populations of mysids and amphipods in the lagoon with those offshore. Given the various uncertainties in estimating season production of primary producers and consumers, the standing stocks are in rough balance with energy inputs. The large rates of immigration of mysids and amphipods into the lagoon compensates the predation by apical organisms and the primary production is rapidly grazed. Nevertheless growth rates of phytoplankton are low, as evidenced by low primary productivity and a long

(34 day) turnover time for standing stocks. This argues for a large advective input of phytoplankton and there is evidence that this process is important. Alexander *et al.* (1975) found generally higher rates of primary production in off-shore deeper (>2 m) water and the rapid dilution of freshwater inflow during the open water season requires a short mixing time. Mungall (1978) estimated exchange times as short as 24 hours for the lagoon water under strong wind conditions due to the rapid longshore transport.

We can thus conclude that in situ and advected primary production drive the lagoon ecosystem. Primary productivity in the lagoon is low but possibly sufficient to sustain the grazer biomass without additional inputs. However, advection and mixing of offshore deeper water with lagoon water provide a major supplement to faunal food requirements. The low salinity of the lagoon and the stresses imposed on phytoplankton by the euryhaline water may result in more rapid sinking rates in plant cells. The accumulation of phytoplankton cells at the sediment-water interface may account for the high densities of mysids and amphipods observed there.

V. DISCUSSION

Several lines of evidence indicate that there is a superabundance of food available to fish and birds in Simpson Lagoon during the summer period. Invertebrate studies in the lagoon show that roughly 50 times more food (mysids and amphipods) is available than is required daily by virtually all vertebrate consumers in the system (Griffiths and Dillinger, 1981). This relatively high level of food is maintained through the open-water period. During summer, food is also generally accessible to major predators because the prey is epibenthic in habit (as opposed to infaunal) and the lagoon bottom provides little structural diversity (e.g., rock crevices or vegetated areas) for refuge from predation, although some prey may escape into the detrital mat on the lagoon bottom. Although not elaborated upon in the present report, this high level of food abundance is not restricted to the lagoon environment itself but also occurs in the relatively shallow marine environment seaward of the lagoon (Griffiths and Dillinger, 1981).

The high diet overlap among consumers is also a strong indication that food is superabundant. Overlap is not simply a reflection of a reduced variety of species in the arctic, for there are several sources of food in the lagoon which predators do not appreciably exploit. Few vertebrates eat

molluscs, polychaetes, isopods, tunicates or hydroids, yet these groups comprise a large proportion of the potential supply of food in Simpson Lagoon. Instead, consumers feed primarily on the abundant epibenthic invertebrates and there is a high degree of overlap among consumer diets. Because the available food supply is not finely partitioned by the predators, the implication is that there is a lack of competition for food in the nearshore environment. Had food resources been in limited supply, general ecological theory holds that competition for food would be high and therefore we should observe specialized and non-overlapping feeding habits among predators. Such specialization has in fact been documented in other species-poor ecosystems in non-lagoon waters of the Arctic (Tyler, 1978) and Antarctic (Targett, 1981).

Some exceptions to the foregoing pattern of diet overlap occur in Beaufort Sea coastal waters. Fourhorn sculpin, for example, eat more isopods than other consumers, and boreal smelt eat more fish. Differences in the sizes, shapes and positions of fish mouths of different species also indicate a degree of feeding specialization among nearshore fishes. Despite these differences, the epibenthic food resource remains the principal diet of most fishes.

Some consumers also display differences in feeding habitat preferences. However, recognition of this partial partitioning of lagoon habitat should not obscure the point that

the lagoon's supply of epibenthos (especially mysids) is highly dependent on immigration or dispersal from outside areas (Griffiths and Dillinger, 1981). Thus, both the oldsquaw ducks (which feed mainly in open lagoon waters) and fish (which probably feed near shorelines) are feeding on the same food supply but at different points along its pathway through the lagoon.

Can the premise that food is superabundant be extrapolated to other nearshore areas along the Beaufort Sea coastline? The available data suggest that the kinds of fish using Simpson Lagoon are generally similar to those all along the Beaufort Sea coastline, and at all locations studied the fish rely on epibenthic invertebrates as their principal food resource (e.g., Kendel *et al.*, 1975; Furniss 1975; Griffiths *et al.*, 1975, 1977; Bendock, 1977). However, it is premature to extrapolate the 'food superabundance' premise to other localities or even other years. In August 1978, an event occurred in Simpson Lagoon which suggested that fish may, on occasion, reduce the food supply to low levels. The event was the brief entry into the lagoon of a large school of arctic cod. They consumed a large quantity of mysids during their nine-day visit and this may have contributed to a decline in mysid densities at this time. This decline did not substantially affect the food base, but it is conceivable that the large school of cod, given its estimated size and food consumption

rate, could have seriously depleted the lagoon's food supply if it had remained in the lagoon an extra two weeks or so.

A second note of caution is that a high incidence of empty fish stomachs has been recorded at some coastal locations (summarized in Craig and Haldorson, 1981). While the occurrence of empty stomachs may reflect a number of factors (e.g., diel periodicity in feeding, regurgitation or digestion of food after fish capture, reduced feeding for anadromous fish on return migration to fresh water), the data also are consistent with either of two very different interpretations: (1) fish may not have to feed continuously in order to satisfy their nutritive requirements, or (2) fish are not getting enough to eat at some locations or in some years.

A. *Factors Contributing to Food Abundance*

1. *Immigration.* Despite the large standing stocks of epibenthos in Simpson Lagoon in summer, birds and fish could theoretically consume the entire stock within 2-6 weeks. But a steady decline of food does not occur -- the food supply is maintained at its relatively high level throughout the summer, despite an increase in consumer demand as the summer progresses. Potential reasons are growth of the invertebrates present in the lagoon and/or immigration of new invertebrates into the lagoon. Reproduction does not occur during summer. Griffiths and Dillinger (1981) show that

immigration is by far the more important. *Mysis litoralis*, the major prey species, moves into the lagoon in early summer; this 'inoculation' and the continuing immigrations that follow, are critical events for the fish and birds. Thus, we see that shallow nearshore habitats become 'food rich' only after being repopulated each year by key invertebrates and remain food rich only by continued immigration. If these immigrations are obstructed by either natural events or man-caused structural alterations in the nearshore environment, the lagoon might remain a poor feeding area for that particular summer.

Productivity in Simpson Lagoon is linked to offshore areas in even a more fundamental way. Isotopic studies of organisms collected in the lagoon indicate that fish ultimately obtain 80-90% of the carbon in their tissues from modern marine primary production (Scheff *et al.*, 1982). Relatively little of the large input of terrestrially-derived organic carbon appears to enter trophic pathways leading to birds and fish in the marine ecosystem (but note Scheff's (1982) discussion about the role of peat in the freshwater ecosystem). This finding underscores the importance of the relationships between the lagoon and outside marine waters.

2. *Seasonally Limited Availability.* A factor that contributes to the abundance of epibenthos is that these inver-

tebrates are not accessible to most vertebrate consumers for almost nine months of the year. Birds and anadromous fish have the opportunity to eat them only during the short open-water period. Marine fish, however, have almost year-round access to the epibenthos, although not in shallow lagoon waters.

3. *Habitat Disturbance.* Ecological succession, the orderly process of community change, is maintained at an early stage in Simpson Lagoon. The lagoon is a 'pioneer community' because periodic physical disturbance permits relatively few invertebrate species to occur as permanent residents. Several features of the lagoon make life difficult. The lagoon is essentially a shallow, wind-churned and turbid channel of water. Its nearly featureless bottom is covered with an unstable mud-sand substrate -- an environment that typically supports a low diversity of organisms. Summertime water temperatures and salinities are highly variable and a rapid flushing rate insures that the system is influenced by events outside its borders. In winter, portions of the lagoon freeze solid and little free water remains under the ice elsewhere; at this time water may become hypersaline. In springtime, there may be some ice-gouging of substrates as well as rapid and extreme fluctuations in salinity. All in all, the lagoon requires that organisms cope with fluctuating

physical conditions on both daily and seasonal bases.

Species diversity in early successional stages is typically low but those species present are often represented by very large numbers. In Simpson Lagoon, it appears that the numerical success of the **epibenthic** invertebrates may be attributed to their mobile **life** style and tolerance of a wide range of physical conditions. Mobility is an essential asset; it allows **mysids** and **amphipods** to repopulate annually the nearshore that freezes solid each winter. These invertebrates are widespread and seem to utilize virtually the entire nearshore zone. They are tolerant of the wide ranges of water temperature and salinity (Busdosh and Atlas, 1975; Broad *et al.*, 1979) that occur in the nearshore environment. As a generalization, the **epibenthic** invertebrates share attributes with 'colonizing species' -- species that are **characteristically** the **first** occupants in recently disrupted habitats. Williams (1969) describes colonizers as 'versatile **species-creatures** of the ecotone, physiologically and ecologically tolerant of many conditions and requiring of few'.

The contention that Simpson Lagoon is a 'disrupted' environment due to widely fluctuating physical conditions is reflected by the high degree of food overlap among consumers. As natural (or human) disturbance to an ecosystem increases, the amount of dietary overlap also increases (Tyler, 1978).

Tyler found that overlap is low in systems that are physically constant. In Dease Strait, a deep-water arctic area with year-round constant temperatures and almost year-round ice-cover, the assemblage of fishes has a very strong partitioning of food resources (low overlap). In contrast, fishes from physically disturbed habitats tend to have a weak partitioning of food resources (high overlap). This relationship is shown in Figure 11. Tyler suggests that regularly repeated perturbations to a system would allow the persistence of high turnover r-type species (Gadgil and Solbrig, 1972) in abundance, accompanied by weakening of food resource partitioning and co-existence of predators that would otherwise not be possible.

To compare the Simpson Lagoon data with Tyler's findings, the percent overlap was calculated from principal prey diagrams (Fig. 7) since this was the method used by Tyler (1978). For the summer of 1977, there are 7 entries of principal prey (R rows) and 6 consumers (C columns). The possible number of recurrences of principal prey in consumer diets is $R \times (C-1)$ or 35. Since there are 11 actual recurrences, the overlap was $11/35 = 31\%$. There was a 50% overlap the following summer. Analyzed in this fashion, Simpson Lagoon falls into the category of 'most disturbed' habitat during the summer months (Fig. 11).

In winter, one might predict that overlap would be low

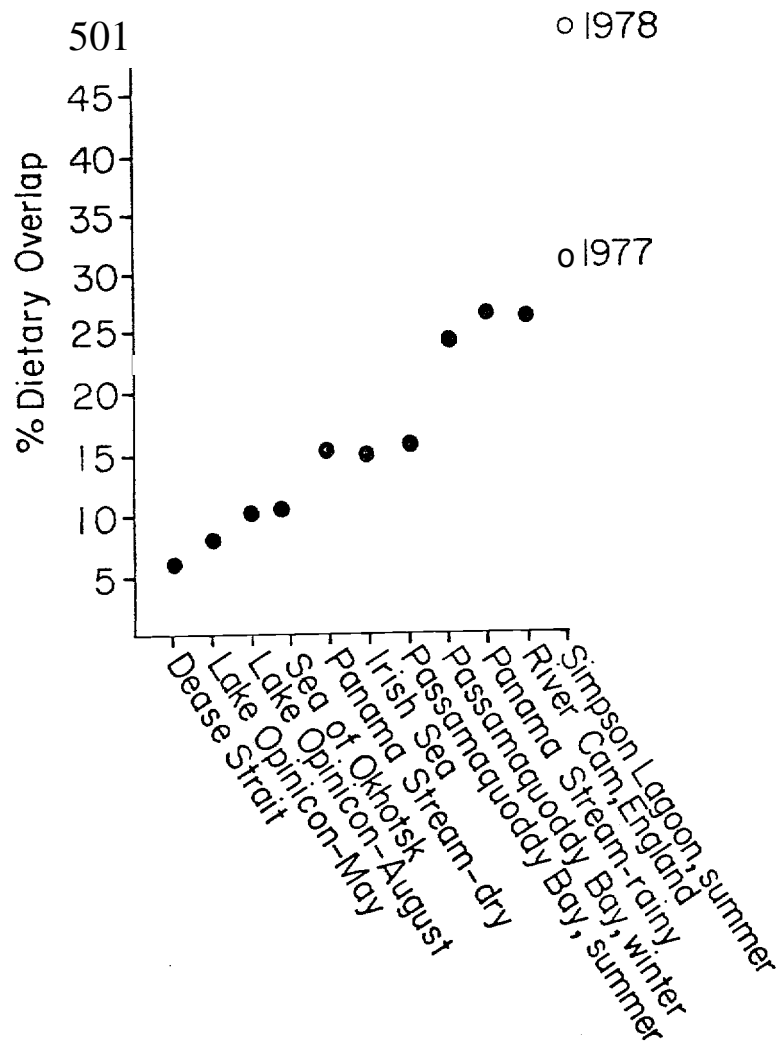


FIGURE 11. Relationship between dietary overlap among vertebrate consumers and the degree of habitat disturbance in the system (Tyler, 1978). Data are ranked by percentage overlap; solid dots indicate overlap among fish communities at various locations, and open circles indicate overlap among major consumers (fish and birds) in Simpson Lagoon, summers 1977 and 1978. Redrawn from Tyler (1978).

since ice-cover would presumably dampen physical fluctuations; however, the widely separated overlap values obtained at different places and times during this period make interpretation difficult. Overlap was low in coastal waters (10%, 1978-79 winter) but high in the Colville Delta (50%, 1977-78 winter). Reasons for this difference are not known but may reflect several factors (e.g., different fish species, different habitats, small sample sizes). In any case, it is interesting that the low overlap in coastal waters for winter-caught marine fish is similar to that obtained by Tyler for summer-caught marine fish from deeper arctic waters.

In summary, it would appear from several different viewpoints that Simpson Lagoon is a rigorous habitat due to fluctuating physical factors (substrate, gouging and resuspension, turbidity, salinity and periodic freezing). This, in turn, suggests that -- at least in summer -- the few species successfully tolerating these conditions would not be *overly* sensitive to related types of small-scale perturbations to the physical environment which might result from petroleum-related activities.

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